
PHYLOGENY AND SPECIATION IN *LAPEIROUSIA* SUBGENUS *LAPEIROUSIA* (IRIDACEAE: IXIOIDEAE)¹

Peter Goldblatt² and
John C. Manning³

ABSTRACT

A cladistic analysis of southern African subgenus *Lapeirousia*, one of two subgenera of the exclusively African genus *Lapeirousia*, yielded four equally parsimonious trees, one of which is identical with the strict consensus tree. Characters used in the analysis included growth form, corm morphology, a range of floral characters, and capsule and seed features, not before known to vary significantly in this genus. The analysis suggested some surprising evolutionary changes. Notable among these is an apparent reversal of perianth tube length from extremely long to short, a shift corresponding to a change from pollination by long-tongued flies and sphinx moths to pollination by bees and noctuid moths. Another unusual change is a shift in floral organization from zygomorphy to actinomorphy correlated with an acaulescent growth form. The reconstructed phylogeny is used here to assess character evolution and patterns of speciation by comparison of species in terminal clades in the cladograms. The resulting comparisons suggest that speciation in the subgenus is either allopatric or the result of microgeographic differentiation and ecological diversification stimulated by edaphic diversity. Despite the variety of floral forms and pollination syndromes in the subgenus there is no evidence of sympatric or pollinator-driven speciation. Prepollination reproductive isolation appears to be achieved by shifts in pollination syndromes between sphinx moths, two guilds of long-tongued flies, and bees. The remarkable floral divergence that has resulted appears to be a consequence of selection for repeated entry into preexisting pollination guilds. The most important of these pollination guilds are two long-tongued fly guilds in which either *Prosoeca* (Nemestrinidae) or *Moegistorhynchus* (Nemestrinidae) and *Philoliche* (Tabanidae) are pollinators. These two guilds are also likely to have been important in promoting speciation in other genera and families in the southern African flora.

The flora of southern Africa is rich and unusually diverse for an area falling predominantly in temperate latitudes (Goldblatt, 1978). Some 20,400 species of native vascular plants are currently recognized in the region (Arnold & de Wet, 1993), of which about 80% are endemic (Goldblatt, 1978). The major factors proposed to account for the species richness are climatic, edaphic, and topographic diversity and a history of paleoclimatic change in the late Tertiary (Goldblatt, 1978). Although these factors may permit the existence of large numbers of species, they do not indicate the modes of speciation that have led to this diversity. One method of inferring modes of speciation is by comparing biological attributes of closely related, and by extension evolutionarily recent, sister species. Differences in biology between such species give an indication of the factors that led to speciation. Cladistic analysis is a critical method for identifying sister species. A detailed phylogenetic hypothesis such as a cladogram makes it possible to trace backwards in time the series of evolutionary events

that gave rise to the modern taxonomic distribution of ecological features even in the absence of fossil information (Armbruster, 1993). This in turn makes it possible to develop specific hypotheses on the evolution of species diversity (Manning & Linder, 1992).

The tropical and southern African genus *Lapeirousia* Pourret comprises some 40 species segregated in two subgenera each with two sections (Goldblatt & Manning, 1990, 1992, 1994). Subgenus *Lapeirousia* (21 species) is centered in coastal and near interior southwestern Africa. This is a semiarid region of low to moderate winter rainfall and extreme summer drought. Two species are widespread in the southwestern and southern parts of Western Cape Province, South Africa, and a further two occur in tropical Africa (Goldblatt, 1990b). Subgenus *Paniculata* (19 species) comprises the largely tropical African section *Paniculata* (14 species), with one species in the southwestern part of southern Africa (Goldblatt & Manning, 1992), and section *Fastigiata* (5 species), which is restricted

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² B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

³ Compton Herbarium, National Botanical Institute, Kirstenbosch Botanic Gardens, Claremont 7735, South Africa.

to the southwestern part of Western Cape Province. Field studies of subgenus *Lapeirousia* conducted over the past three years have provided a wealth of information about the ecology and biology of its 21 species, and this has enabled us to develop a detailed understanding of the group. This has provided an objective measure of relationships among the species that in turn lays the foundation for analyses of changes in pollinator preferences and patterns of radiation and speciation. We use the reconstructed phylogeny of subgenus *Lapeirousia* and the inferred modes of speciation to address questions of how its species coexist and how they might have evolved. We expect these hypotheses to have more general application for plant speciation in southern Africa.

MATERIALS AND METHODS

CHARACTERS AND TAXA

Subgenus *Lapeirousia* is believed to be monophyletic and the sister clade to subgenus *Paniculata* (Goldblatt & Manning, 1990), the outgroup for the cladistic analysis. The subgenus is regarded here as comprising 21 species (Goldblatt, 1972, 1990b; Goldblatt & Manning, 1994). Both subspecies of *L. pyramidalis* (subsp. *regalis* and subsp. *pyramidalis*) are included in the analysis because they differ in some important characters, and we were unwilling to assign arbitrary plesiomorphic states for the species. Morphological and anatomical characters (Table 1) were assembled from the above systematic treatments, and supplemented by new data presented here.

For the cladistic analysis 24 characters were ultimately selected (Table 1; Appendix). These included all macromorphological aspects of the plants, as well as capsule and seed surface morphology, not known until now for most species. Seed characters of all species of *Lapeirousia* were investigated for this study. Seeds vary both in primary and secondary sculpturing, and provided valuable characters for the cladistic analysis (Appendix: characters 6, 7, and 8). Chromosome cytology (Goldblatt & Takei, 1993) was not included in the cladistic analysis, but was used to assess the trees that were generated. Basic chromosome number for *Lapeirousia* is probably $x = 10$, but the base number for subgenus *Lapeirousia* appears to be $x = 9$ (Goldblatt, 1990a; Goldblatt & Takei, 1993). Multistate characters of an additive nature, e.g., corm tunic bases lobed, lightly denticulate, coarsely dentate, were treated as ordered (characters 2, 6, 7, and 14).

ECOPHYLOGENY

Data on pollination and habitat were recorded for each species in subgenus *Lapeirousia* and mapped onto the cladogram (Fig. 4). The ecological characteristics of the lower nodes were determined using the operating principle of parsimony. In this way the evolutionary history of the interactions can be inferred and the sequence of evolutionary changes that have generated the current interactions can be determined (Donoghue, 1989; Brooks & McLennan, 1991; Armbruster, 1992). This methodology has been used to investigate the evolution of pollination systems in, for example, *Dalechampia* (Euphorbiaceae) (Armbruster, 1992, 1993, 1994). Data on pollination ecology are derived from Goldblatt et al. (1995).

CLADISTIC ANALYSIS

Data were analyzed using the Hennig86 package of programs for parsimony analysis (Farris, 1988), using the mh* and bb* option, followed by successive weighting. Five randomly generated taxon sequences were analyzed, with the same result being obtained. The data include considerable homoplasy (there appear to be convergent trends for some flower types in different lineages) with the result that the strict consensus tree of 1322 equally parsimonious trees resulting from unweighted computations (Fig. 1A) shows little resolution (length 74, consistency index (CI) 0.48, retention index (RI) 0.67).

Successive weighting, recommended by Farris (1969) for situations where unreliable (homoplasious) characters outnumber reliable characters, is one way to improve tree resolution. The method selectively weights those characters that are more consistent at the expense of those that are homoplasious. The method can be successful even when cladistically consistent characters are heavily outnumbered by homoplasious ones. After invoking the successive weighting option six equally parsimonious trees (CI 0.81 and RI 0.91), but only four different topologies, were obtained. The four trees differ only in minor details and correspond in most respects to our intuitive ideas about species relationships in the subgenus. The strict consensus tree obtained with successive weighting (Fig. 1B) is actually identical to one of the four final trees (Fig. 2A), and discussion is framed around this tree.

All the differences in branching patterns in the other trees are present in a second tree illustrated (Fig. 2B). The differences are alternative topologies at nodes 7 and 14. We generated one more tree using the data matrix and the same options, mh*, bb*, and successive weighting, but with *Savanno-*

Table 1. Matrix and character list for the cladistic analysis (Figs. 1–3). The outgroups are *Savannosiphon* or subgenus *Paniculata*. The features of the latter are inferred by comparison of its constituent species (no single species accords with the hypothetical ancestor). When the plesiomorphic state is uncertain for the outgroup, the character is scored as “?”. Chromosome numbers were not included in the analysis, but where confidently known (Goldblatt & Takei, 1993), are indicated opposite each species in Figure 4. Character 25 is used only with the analysis with *Savannosiphon* as the outgroup (Fig. 3). Multistate characters 2, 6, 7, and 14 are treated as ordered (see Appendix 1), and 5, 8, 13, 15, and 17 are treated as unordered.

Taxon	Character number				
	123456	111 789012	111111 345678	122222 901234	2 5
<i>Savannosiphon</i>	0?0100	100000	201000	0010?0	0
Subgenus <i>Paniculata</i>	000?00	000000	000000	000000	1
<i>L. pyramidalis</i> (Lam.) Goldblatt					
subsp. <i>pyramidalis</i>	100102	011011	300101	010110	1
subsp. <i>regalis</i> Goldblatt & Manning	100102	011011	303101	010100	1
<i>L. silenoides</i> (Jacq.) Ker Gawl.	100101	011011	303101	110000	1
<i>L. verecunda</i> Goldblatt	100101	011011	302101	110000	1
<i>L. divaricata</i> N. E. Br.	120101	020111	111021	110011	1
<i>L. spinosa</i> (Goldblatt) Goldblatt	120111	001111	111021	1100?1	1
<i>L. dolomitica</i> Dinter	131101	001011	303011	010000	1
<i>L. violacea</i> Goldblatt	131101	001011	303010	110000	1
<i>L. tenuis</i> (Goldblatt) Goldblatt & J. Manning	131101	000011	10001?	110000	1
<i>L. jacquinii</i> N. E. Br.	110101	021011	303010	110100	1
<i>L. fabricii</i> (Delaroché) Ker Gawl.	121101	020111	222010	111000	1
<i>L. barklyi</i> Baker	111101	000111	023020	111000	1
<i>L. simulans</i> Goldblatt & Manning	110101	000011	302010	110000	1
<i>L. macrospatha</i> Baker	110111	021011	202010	011000	1
<i>L. arenicola</i> Schltr.	110111	021011	202000	110000	1
<i>L. littoralis</i> Baker	100100	101011	301000	?11010	1
<i>L. anceps</i> (L.f.) Ker Gawl.	100101	000011	302010	110000	1
<i>L. odoratissima</i> Baker	100020	101011	301000	011010	1
<i>L. montana</i> Klatt	100020	201011	300000	010010	1
<i>L. plicata</i> (Jacq.) Diels	100020	101011	200000	010000	1
<i>L. oreogena</i> Schltr. ex Goldblatt	100020	201011	303000	010000	1
<i>L. exilis</i> Goldblatt	100111	001011	200100	?10000	1

1. Corm tunics consisting of compacted fibers (0)—corm tunics woody (1)
2. Corm tunic bases lightly lobed (0)—bases minutely denticulate (1); bases coarsely and irregularly short-dentate (2); bases fairly regularly long-dentate (3)
3. Corm shape campanulate (0)—corm shape broadly conic (1)
4. Flowers actinomorphic (0)—flowers zygomorphic (1)
5. Plants with well-developed aerial stems (0)—plants forming fairly compact tufts (1); plants normally without aerial stems, i.e., acaulescent (2)
6. Seed surface cells unevenly colliculate-foveate and not in straight files (0)—cell surfaces colliculate and cells in files (1); cell surfaces tuberculate and cells in files (2)
7. Seed surface without secondary sculpturing (0)—surface with folds in a diffuse ruminant pattern (1); surface with a \pm regularly reticulate pattern (2)
8. Capsules rounded in transverse section, thus without locular ridges (0)—capsules with winglike locular ridges (1); capsules with auriculate lobes decurrent on locular ridges (2)
9. Branches borne well above the ground (0)—branches mostly or only at ground level (1)
10. Lower tepals straight (0)—lower tepals geniculate (1)
11. Leaf blades plane (0)—blades plicately ribbed (1)
12. Bracts soft-textured (0)—bracts firm-textured (1)
13. Perianth tube about as long as the tepals (0)—shorter than the tepals (1); 1.5–3 times as long (2); (3–)4–6 times as long (3)
14. Perianth tube \pm cylindrical throughout (not abruptly widened above) (0)—tube abruptly expanded above into a flared upper part (1); tube with the upper part wide and cylindrical (2)

Table 1. Continued.

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15. Perianth pale blue with white and dark blue markings (0)—predominantly white (sometimes with cream or blue markings) (1); cream with red markings and reddish on the reverse (2); dark red to purple or blue to violet (3)
 16. Tepals ovate to lanceolate (0)—tepals spatulate (1)
 17. Surface of lower tepals plane (0)—lower tepals each with a slender cusp near the base (1); lower tepals each with a toothlike ridge at base (2)
 18. Upper tepal reflexed (0)—upper tepal arched (1)
 19. Outer bracts without a median fold or keel (0)—outer bracts with median fold or keel (1)
 20. Inner bracts about as long as the outer (0)—two-thirds to half as long (1)
 21. Flowers small (upper tepal usually less than 16 mm long) (0)—flowers large (upper tepal 18–27 mm long) (1)
 22. Outer bracts acute (0)—bracts obtuse to retuse (1)
 23. Flowers unscented (0)—flowers sweetly scented (1)
 24. Lower and upper lateral tepals separating from the tube at the same level (0)—lower tepals joined to the upper laterals for 3–5 mm (1)
 25. Corm base rounded (0)—bases flat, corm thus campanulate (1)
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siphon as the outgroup, and one more character, campanulate corms, the generic synapomorphy for *Lapeirousia* (Fig. 3). Because *Savannosiphon* has been suggested to be the sister genus to *Lapeirousia* (Goldblatt, 1989) we were curious to see how the resulting trees would compare with those in which subgenus *Paniculata* is the outgroup. Trees were analyzed using CLADOS (Nixon, 1992) and the trees presented here were generated with this program.

The phylogenetic relationships were also reconstructed using PAUP 3.1.1 (Swofford, 1993) in order to utilize the bootstrap option and establish a measure of confidence in the results of the cladistic analysis (Felsenstein, 1985). A heuristic search was carried out saving minimal length trees only with the collapse zero length branches option in effect. The data were subjected to reweighting, using the maximum value of rescaled consistency indices, which is the same as successive weighting in Hennig86 (Swofford, 1993). A hundred replicates were run with the heuristic search option (limitations of time made it impractical to run more than 100 replicates), simple weighting, and with characters sampled randomly. The bootstrap values are presented on the strict consensus tree (Fig. 1B).

RESULTS

CLADISTICS

On the trees illustrated (Figs. 2A, B), the character distributions as mapped show subgenus *Lapeirousia* to be supported by seven synapomorphic characters, four of which are autapomorphic and three homoplasious. The subgenus can thus reasonably be presumed to be monophyletic. The autapomorphies for the subgenus include woody corm

tunics, leaf blades with plicate ridges, floral bracts firm-textured, and inner bracts about half as long as the outer (characters 1, 11, 12, 20), all universal for the subgenus. Within subgenus *Lapeirousia* the strict consensus tree indicates a primary divergence into two clades, the smaller one of which (node 2) comprises all the species with derived seeds having primary sculpturing (character 7). The clade, which includes the type of section *Sophronia* (but not all the species assigned to it by Goldblatt & Manning (1990)), also contains the two tropical African species, *L. littoralis* and *L. odoratissima*. Within this clade a group of species are apomorphic in their acaulescent habit and actinomorphic flower, a reversal which may well be closely associated with the acaulescent habit (Goldblatt, 1990b). In addition, all species of the clade at node 2 have the derived basic chromosome number, $x = 8$. Although we see no a priori reason to believe that the clade is an artifact of the analysis, in the strict consensus tree generated using *Savannosiphon* as outgroup, *L. littoralis* is one clade of a trichotomy (Fig. 3) in which the acaulescent species comprise the second clade and the remaining species of the subgenus the third. Close association of the acaulescent species and *L. littoralis* depends on how character 7 (seeds with primary sculpturing) is polarized, and this will remain uncertain until more information can be obtained about the generic relationships of *Lapeirousia*.

The second of the two primary clades (node 5) in both the trees with subgenus *Paniculata* as outgroup has either two synapomorphies (Fig. 2A), seeds with colliculate secondary sculpturing (character 6), and bracts with a median fold or keel

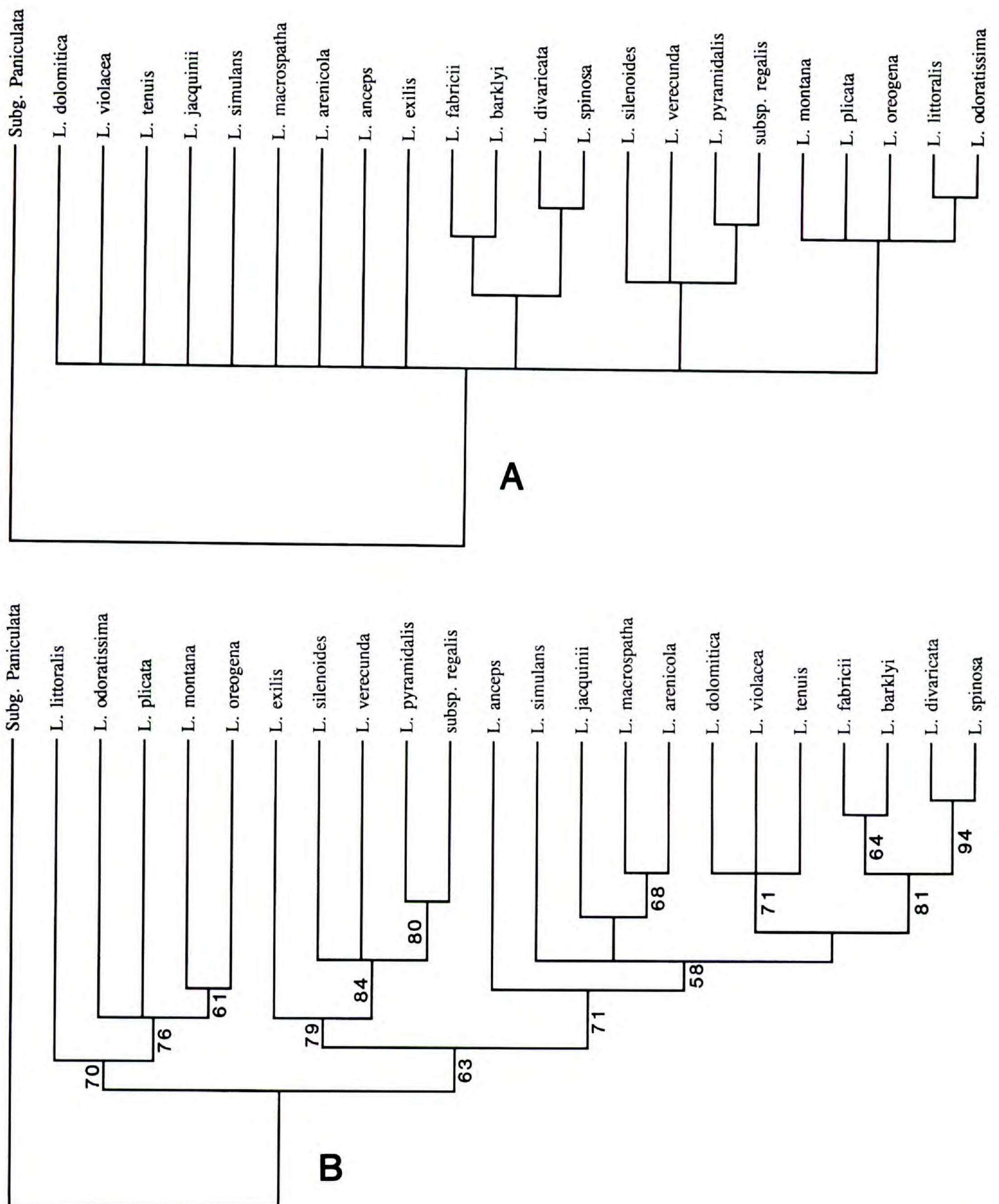


Figure 1. Strict consensus trees generated from the character matrix (Table 1).—A. Tree generated using the mh* and bb* options of Hennig86.—B. Bootstrap values drawn on the strict consensus tree generated using the mh* and bb* options of Hennig86 followed by successive weighting. The bootstrap values were calculated using PAUP and involving the maximum value of rescaled consistency index option (equivalent to successive weighting of Hennig86).

(character 19), or one synapomorphy (Fig. 2B), character 6. Within this clade there is again a primary dichotomy. Of the two resultant clades the one at node 6 is supported by one floral character, the spatulate shape of the tepals. However, the clade

at node 9 has either three characters (Fig. 2A): cusps on the lower tepals (17), perianth cream with red markings (15), and the branching pattern (9), all homoplasious; or four, the last being the outer bracts folded or keeled (19) (Fig. 2B). All members

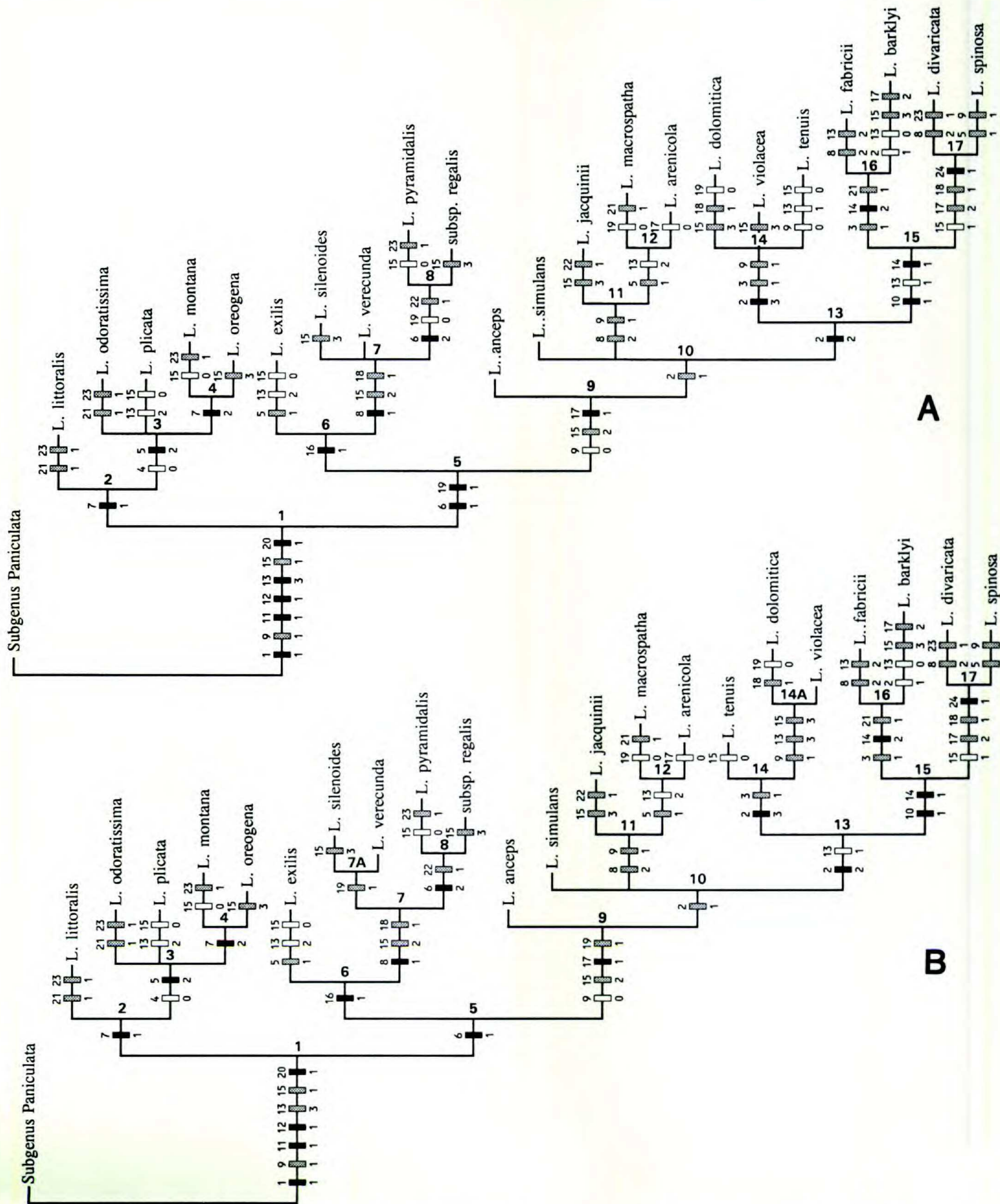


Figure 2. Cladograms generated using the mh*, bb*, and successive weighting options of Hennig86 (Farris, 1988), using the data matrix (Table 1) and subgenus *Paniculata* as outgroup.—A. Strict consensus tree of six equally parsimonious trees. The strict consensus tree is identical to one of the six trees, hence the characters are mapped on the tree.—B. One of the other five trees embodying the two differences between the strict consensus tree and the six original trees, indicated at nodes 7 and 14. Character bars mapped onto the tree are shaded as follows: black = non-homoplasious apomorphy; gray = homoplasious apomorphy; clear = reversal. Numbers above character bars refer to character numbers, those below the bars indicate the character state.

of this clade except *Lapeirousia anceps*, which is sister to the remaining species, and *L. jacquini* are apomorphic in their corms with basal teeth or spines and chromosome numbers. In particular, *L.*

jacquini shows poor resemblance to other members of the clade in gross morphology. It shares apomorphic bracts with *L. pyramidalis*, has the plesiomorphic corm type, and may have a hybrid ori-

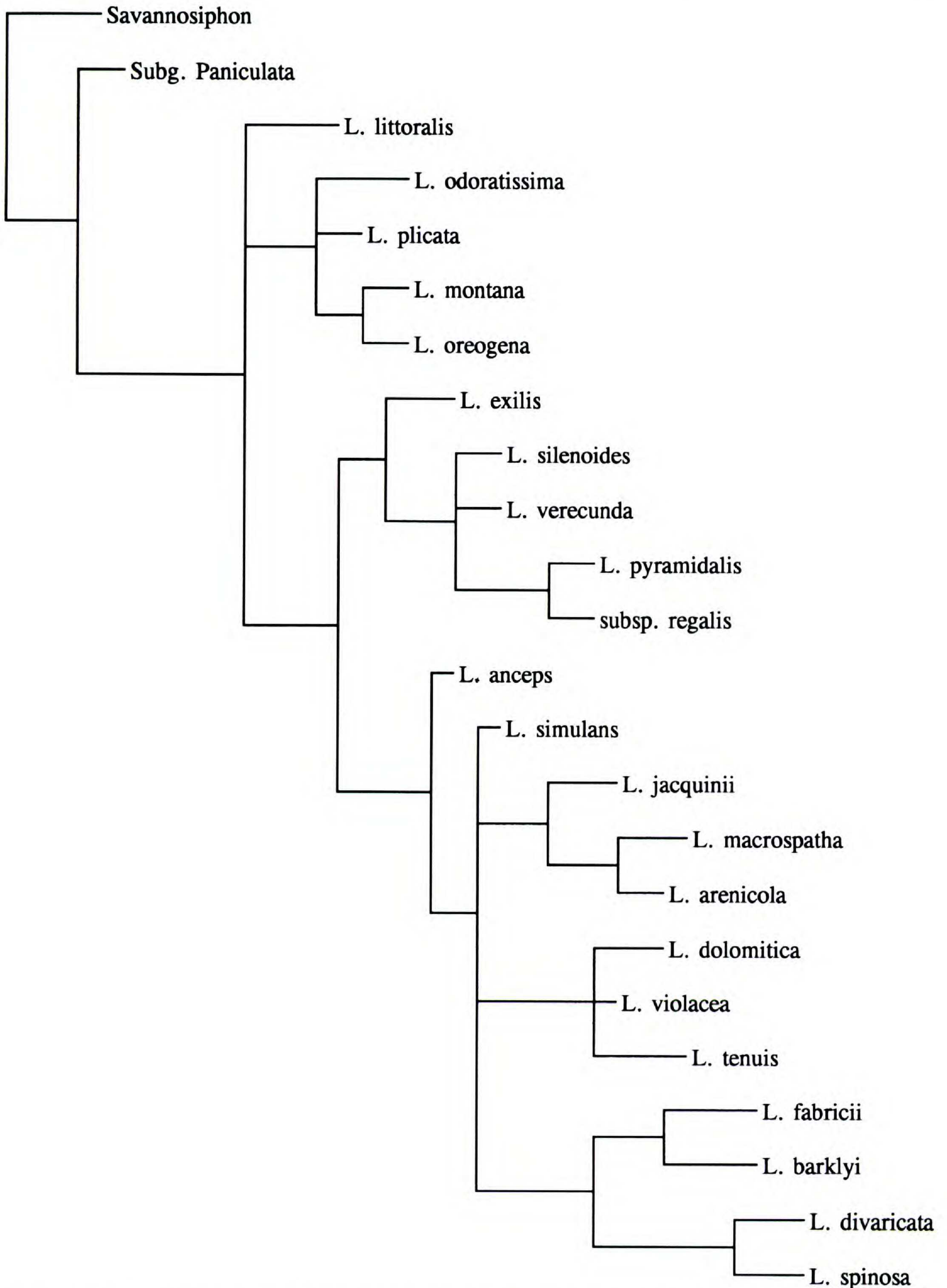


Figure 3. Strict consensus tree of seven equally parsimonious trees generated with the mh*, bb*, and successive weighting options of Hennig86 (Farris, 1988) with *Savannosiphon* as outgroup. The tree was generated using the same data matrix (Table 1) as the trees in Figures 1 and 2, plus one character, campanulate corms, apomorphic for all species of *Lapeirousia*. Scoring was changed for character 7, to reflect changed polarity.

gin. The topology of the remaining species of the clade is consistent with our intuitive ideas about relationships.

Terminal pairs in the strict consensus tree (Fig. 2A) and in the alternative equally parsimonious tree (Fig. 2B) are identical, except for *Lapeirousia silenoides*-*L. verecunda* and *L. dolomitica*-*L. violacea* (compare the topology at nodes 7 and 14 in Figs. 1 and 2). These species are terminal pairs only in Figure 2B. The number of steps to achieve the different topologies is the same (although the characters themselves differ), but we have no a priori reason to favor either alternative. The possibility that the species are terminal pairs remains a reasonable hypothesis. In the tree with *Savannosiphon* as outgroup (Fig. 3) the tree topology is the same at all the major nodes except for the position of *Lapeirousia littoralis*, discussed above. The terminal taxon pairs are the same as in Figure 2A.

Bootstrap values (Fig. 1B) calculated with PAUP and based on a heuristic search with 100 replicates (Swofford, 1993) are drawn on the strict consensus tree obtained using Hennig86. Values above 70% are believed to have a 95% confidence level (Hillis & Bull, 1993). Values calculated for our trees range from 58% to 94%. The five terminal species pairs in the consensus tree have bootstrap values of 61% and higher. These values lend support to our speculations about evolution and speciation in terminal clades obtained by the cladistic analyses and allow us to frame hypotheses about the mechanisms of speciation in subgenus *Lapeirousia*. Ultimately we hope that the hypotheses about phylogenetic relationships presented here will be compared with phylogenetic reconstructions based on independent molecular methods of DNA sequencing or restriction enzyme analysis.

The phylogenetic analysis does not support our previous division of subgenus *Lapeirousia* into two sections (Goldblatt & Manning, 1990). In this classification species of section *Sophronia* fall in two major clades, those above nodes 2 and 6 (Fig. 1). Section *Lapeirousia*, however, corresponds to the clade above node 9. A preferable classification for the subgenus would be to restrict section *Sophronia* only to the species above node 2 and to recognize a third section for those at node 6, thus according sectional rank to the three major clades (Fig. 1) of the subgenus. A revised sectional classification based on our phylogenetic analysis will be included in a taxonomic revision of *Lapeirousia* currently in preparation.

SPECIATION MECHANISMS IN TERMINAL TAXA

There are five terminal pairs (Fig. 2A: nodes 4, 8, 12, 16, and 17) available for analysis on the

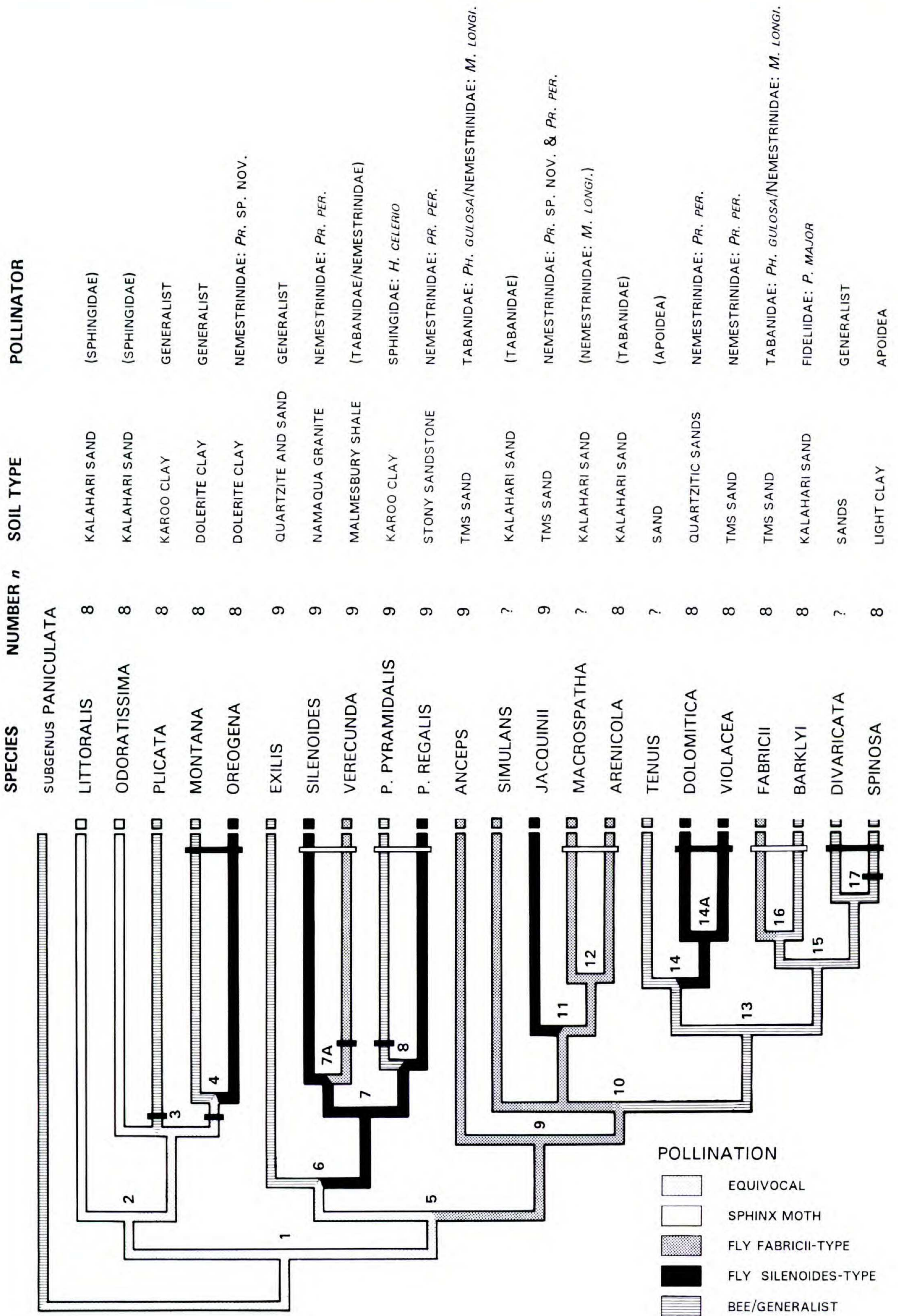
Table 2. Distribution of differences (indicated by an asterisk, *) among taxa of terminal sister groups. Inferred differences in parentheses. 4 = *L. oreogena-montana*; 7A = *L. silenoides-verecunda*; 8 = subsp. *pyramidalis*-subsp. *regalis*; 12 = *L. macrospatha-arenicola*; 14A = *L. dolomitica-violacea*; 16 = *L. fabricii-barklyi*; 17 = *L. divaricata-spinosa*.

	Node						
	14A	4	7A	8	12	16	17
Allopatry	*	*	—	—	—	—	*
Parapatry	—	—	*	*	*	*	—
Soil type	*	—	*	*	—	*	*
Pollinator	—	*	(*)	*	(—)	*	—

consensus tree obtained by successive weighting, and three of these are present on the unweighted consensus tree. The alternative hypothesis provides two more pairs (Fig. 2B: node 7A, 14A, the last one present in more than half of the most parsimonious trees). Moreover, these last two pairs are members of species trichotomies in the trees in which they are not terminal pairs. For analysis of biological differences, we compared the biology of the species at the terminal nodes to assess the factors that might have led to speciation of these pairs. The environmental determinants taken into account in this analysis are spatial separation, edaphic differences, and pollinator divergence (Table 2). There is no separation in flowering time between the species in any of the pairs available for analysis (Goldblatt et al., 1995).

A geographical component (Fig. 4) is present in all of the terminal pairs and the sister species are either allopatric, i.e., separated by a significant geographic distance (nodes 4, 14A, and 17), or parapatric, i.e., their ranges are adjacent although they do not grow intermixed (nodes 7A, 8, 12, and 16). In addition, members of most species pairs occur on a different soil type (nodes 7A, 8, 14A, 16, 17, but not those at nodes 4 and 12). Pollinator divergence characterizes three of the four parapatric species pairs (nodes 7A, 8, and 16) but only one of the allopatric pairs (node 4).

There are floral differences between the species in all the terminal pairs except at node 17 (*Lapeirousia divaricata* and *L. spinosa*). These differences are substantial at node 16 (*L. barklyi* and *L. fabricii*), involving morphology and markings, and accompany a shift in floral type and pollination syndrome between fly and bee pollination. Floral differences are less marked at nodes 4, 7A, 8, 12, and 14A and largely involve pigmentation and small changes in tube length. These relatively mi-



nor differences in floral features either accompany a change in pollinator species within the same general pollination syndrome (fly pollination) (node 7A), or a shift between fly and generalist pollination (nodes 4, 8, and 16), or are not accompanied by shifts in pollinator at all (nodes 12 and 14A). Differences between the allopatric *L. divaricata* and *L. spinosa* (node 17) and the parapatric *L. arenicola* and *A. macrospatha* are mainly vegetative, and no change in pollination system is involved.

Speciation in subgenus *Lapeirousia*, as far as can be assessed by comparing the terminal pairs in the cladogram, thus appears to be exclusively geographic, either allopatric or parapatric. Speciation is usually combined with specialization for a different soil type, and a shift in pollinator typically accompanies the speciation event in three of the four parapatric pairs but not in allopatric pairs (Table 2). Significant changes in flower architecture accompany shifts between bee and fly pollination. Only minor or no floral changes at all occur in shifts within a single pollination system.

HISTORICAL ANALYSIS

There are three potential problems with the ecophylogenetic method for analyzing the evolutionary history of ecological features (Armbruster, 1992): stability of cladogram topology, completeness of ecological data, and circularity of reasoning. The reconstructed phylogeny of subgenus *Lapeirousia* is generally well supported (Fig. 1B), and the ecology of nearly all species is known (see Fig. 4). The edaphic hypothesis is free from the danger of circular reasoning because soil preferences were not used to reconstruct the phylogeny. There is, however, a possibility for circularity of reasoning regarding the evolution of pollination types because a number of floral characters of obvious adaptive value in pollination were used to generate the phylogeny. These are perianth tube length (character 13), perianth color (character 15), upper tepal orientation (character 18), and presence or absence of fragrance (character 23). In the absence of data independent of the ecological data being analyzed, Armbruster (1992) has suggested that the indepen-

dence of characters used can be assessed a posteriori by checking for high consistency between the phylogeny and the ecological feature under consideration.

In subgenus *Lapeirousia* the phylogeny and pollination system are poorly correlated suggesting that there is no circular relationship between the two. The consistency indices for the four characters related to pollination type are 0.25, 0.16, 0.33, and 0.20, respectively. These are at the lower end of the scale for morphological characters (0.20 to 1), unrelated to pollination system, and also argue against any circularity in our analysis. Another challenging test of the ecophylogenetic hypothesis is to generate predictions based on the hypothesis and compare the predictions with new observations (Armbruster, 1992). In subgenus *Lapeirousia* our ecophylogenetic hypothesis includes the inference that the *L. silenoides*-type long-tongued fly pollination (Goldblatt et al., 1995) has evolved repeatedly. A prediction of this hypothesis is that the specialized corollas in these lineages differ from one another in detail, although they are functionally and superficially similar. This is indeed the case (see below). The ecophylogenetic hypothesis about evolution of pollination systems in subgenus *Lapeirousia* is thus supported by all three tests.

EDAPHIC DIVERSIFICATION

Species of subgenus *Lapeirousia* show nearly complete substrate fidelity. It is most parsimonious to assume that coarse and sandy soil in general (four changes) rather than fine clay (five changes) was the substrate favored by the species ancestral to subgenus *Lapeirousia*, although it is not possible to infer whether this was Kalahari sand or Table Mountain Series sand (Fig. 4). Comparison of the habitat and distribution of subgenus *Paniculata* (Goldblatt, 1990b) with those of subgenus *Lapeirousia* suggests the former. Ecological diversification to clay soils derived from shales or dolerite occurred within the clades defined by nodes 3 (*L. plicata*, *L. montana*, and *L. oreogena*), 7 (*L. verucunda* and *L. pyramidalis* subsp. *pyramidalis*), and 17 (*L. spinosa*). A single species, *L. silenoides* (node

←

Figure 4. Pollinators, chromosome numbers, soil types, and patterns of allopatry plotted on the historical hypothesis for the evolution of pollination systems in subgenus *Lapeirousia*, derived from the cladogram shown in Figure 2. Long solid bars indicate allopatry; long hollow bars, parapatry; short solid bars, colonization of clay substrates. Pollinators indicated in parentheses are inferred on the basis of floral morphology as detailed by Goldblatt et al. (1995). Pollinator names have been abbreviated as follows: *H.* = *Hippotion* (Lepidoptera: Sphingidae), *P.* = *Parafidelia* (Hymenoptera: Fideliidae), *Ph.* = *Philoliche* (Diptera: Tabanidae), *Pr.* = *Prosoeca* (Diptera: Nemestrinidae), *M. longi.* = *Moegistorhynchus longirostris* (Diptera: Nemestrinidae).

7A), is virtually restricted to Namaqualand granite and granitic sands. Edaphic divergence characterizes five of the seven terminal species pairs and is likely to have provided the initial impetus for genetic differentiation between founder and parent populations.

DIVERSIFICATION OF POLLINATION TYPES

A well-developed floral tube and pale flower appear to be ancestral in the subgenus, and pollination by long-tongued insects may be inferred to be plesiomorphic. The outgroup, subgenus *Paniculata*, is diverse in floral morphology (Goldblatt, 1990b), but the floral types present in subgenus *Paniculata*, coupled with field observations (Goldblatt et al., 1995), suggest that pollination by bees or a combination of bees and Lepidoptera is predominant. Just three species in subgenus *Paniculata* have extremely long floral tubes and display some of the same characteristics as species in subgenus *Lapeirousia* that are known to be pollinated by sphinx moths or long-tongued flies. These species are, however, all believed to be derived in subgenus *Paniculata*, not only because of their derived floral characters but because of their apomorphic karyotypes (Goldblatt & Takei, 1993). Hence, the inference is strong that although both moth and fly pollination are present in the outgroup at low frequencies, these pollination types are independently derived within each of the subgenera.

In subgenus *Lapeirousia*, species richness is not a function of any one pollination strategy. Each of the major clades includes a diversity of pollination systems, and shifts in pollination system have occurred repeatedly. A pale flower (sphinx moth- and *L. fabricii*-type flowers) is evidently plesiomorphic at nodes 4, 6, and 9 (Fig. 4). The inference follows that the *L. silenoides*-type fly pollination (involving *Prosoeca peringueyi* and *P. sp.*), associated with vividly pigmented flowers, was derived four times in the subgenus, at node 4 (*L. oreogena*), node 7A (*L. pyramidalis* subsp. *regalis* and *L. silenoides*), node 14A (*L. dolomitica* and *L. violacea*), and node 11 (*L. jacquinii*). The *L. fabricii*-type fly pollination (involving *Moegistorhynchus longirostris* and *Philolichthe gulosa*) is inferred to have been independently derived three times within the subgenus, at node 7A (*L. verecunda*), and twice in the entire clade at node 9 (Fig. 4). It is most parsimonious to infer a shift to a generalist or bee-dominated system at node 13. In this scenario, a reversal to the *L. fabricii*-type fly pollination system occurred at node 16 (the *L. silenoides*-type fly pollination system evolved at node 14 of the clade). The *L. fabricii*-

type fly pollination appears to be the ancestral pollination system for more than half the species in the subgenus (the entire clade defined by node 9). Bee/generalist pollination appears to be the most derived pollination state in the clade defined by node 9.

Thus, it appears that most of the pollination types found in subgenus *Lapeirousia* have evolved more than once. Bee or generalist pollination has evolved four or five times (node 3 or both nodes 3 and 4, and nodes 6, 8, and 10), *L. fabricii*-type fly pollination three times (nodes 5, 7A, and 16), *L. silenoides*-type fly pollination four times (nodes 4, 6, 11, and 14), and sphinx moth pollination once or twice (nodes 2 or 3 or both). Pollination systems in subgenus *Lapeirousia* are thus evolutionarily labile and prone to parallel evolution and reversal. This applies equally to shifts between bee and fly systems and to shifts between the two fly systems.

The evolution of floral actinomorphy in subgenus *Lapeirousia* coincides with the evolution of an acaulescent habit. Floral actinomorphy is restricted to the species at node 3, all of which are of low stature with a tufted, acaulescent habit. Except for *L. odoratissima* these species grow on clay, and the colonization of more stable clay soils by the ancestor(s) of the remaining species in the clade may have facilitated the diversification of plants with this growth form. Acaulescence has the advantage of retaining the ovules and developing seeds at or below soil level, thus providing protection from the weather and predators (Burt, 1970). The tufted growth form favors vertical flower presentation, and floral actinomorphy is a likely result. A long floral tube enables the flowers to project above the leaf and bracts. The development of long-tubed actinomorphic flowers in subgenus *Lapeirousia* is thus most likely related to plant habit and floral presentation and not to pollinator-driven selection.

DISCUSSION

Our analysis suggests that for the terminal species pairs in subgenus *Lapeirousia* speciation has been exclusively at the diploid level and has mostly involved a combination of shifts in substrate preferences when descendant species occur in adjacent habitats or geographic isolation when the descendant species are separated by significant distance and may or may not occur on different substrates. For the species analyzed the former situation slightly predominates. This pattern is consistent with the hypothesis (Goldblatt, 1978; Linder, 1985; Cowling & Holmes, 1992) that edaphic differences are the predominant cause of species richness in the south-

western part of southern Africa. The isolating effect of discontinuities in substrates (e.g., Kruckeberg, 1986) may in fact be the most significant cause of local and taxonomic diversity. It has been suggested by Linder and Vlok (1991) that each distinctive habitat may represent a "geographic" region without the usual physical barriers associated with allopatric speciation. Such microgeographic or parapatric speciation is particularly likely in the southwestern part of southern Africa where varied soils and topography accompanied by steep precipitation gradients provide a strong selection differential for population divergence and the development of edaphically isolated populations (Goldblatt, 1978; Linder, 1985).

Local divergence between populations, whether linked to edaphic specialization or not, is possible only if gene flow is sufficiently restricted to permit genetic differentiation either by drift or selection. Limited gene flow is typical of most Iridaceae (Goldblatt, 1991), and short gene dispersal distances are a characteristic of most plants in the southwestern part of southern Africa (Cowling et al., 1992). The effect of restricted gene flow is that neighboring populations may be well defined as a result of selective differentials or random drift (Levin, 1981, 1993).

Speciation in subgenus *Lapeirousia* seems to have been initiated by shifts in substrate preference. This has in most instances been accompanied by changes in floral morphology and shifts in pollination strategy, thereby enhancing genetic differentiation initiated by adaptation to different substrates. Edaphic differences in Namaqualand and the northwestern Cape are often associated with other physical differences such as altitude, aspect, and rainfall. They thus signify more profound niche differences than might be suggested by edaphic differences alone. The action of selection on founder populations on novel substrates should be correspondingly stimulated, and would enhance small-scale genetic differentiation. We anticipate that strong selective pressure for the development of prepollination isolating mechanisms would follow the development of these edaphically adapted genotypes at the contact zones between the parent and daughter populations.

In other genera of Iridaceae and some Orchidaceae and Amaryllidaceae small changes in color and scent are sufficient to attract different pollinators and prevent hybridization (Johnson, 1992; Johnson & Bond, 1994; Paulus & Gack, 1990; Steiner et al., 1994). In subgenus *Lapeirousia* the floral changes necessary for a shift between pollination by sphinx moths and long-tongued flies or

between the two types of long-tongued fly pollination primarily involve perianth pigmentation, while those necessary for a shift to bee pollination involve a shortening of the floral tube and sometimes a change in flower color. Both flower color and flower shape are frequently governed by rather simple genetic systems (Gottlieb, 1984; Macnair, 1989). A shorter floral tube is readily achieved through paedomorphosis, while simple heterochronic changes in development may account for other observed floral differences (Guerrant, 1982). In *Aquilegia*, for instance, many of the differences in shape that lead to the attraction of different pollinators are governed by small numbers of genes (Prazmo, 1965).

For the species of subgenus *Lapeirousia* relatively simple mutational or recombinational events might result in a change in flower color from cream to magenta or violet (or vice versa), instantly shifting the plant into a different pollinator guild and effectively isolating it from the parent species. Potentially nonadaptive bottlenecks between pollination systems are thus likely to be small, and pollinator-directed selection for differences in floral morphology should be rapid. This is particularly significant in a situation where floral conformity is as strongly stressed as in the long-tongued fly guilds (Manning & Goldblatt, 1996). Although shifts in pollination system in subgenus *Lapeirousia* involve a complete change in the pollinator species, there can be occasional overlap. For example, we have seen long-tongued fly species visiting short-tubed flowers and some bees occasionally collect pollen from long-tubed species, which they may successfully pollinate. In addition, *Prosoeca peringueyi* has been observed visiting a few individuals of *L. verecunda* at the single known site where the ranges of this species and *L. silenoides* meet. It is thus possible that shifts between the various pollination systems could have occurred with intermediate phases in which both old and new systems operated. Because of the apparently small morphological/genetic changes required for shifts between the various pollination systems in subgenus *Lapeirousia*, the shifts are likely to have been rapid.

We postulate that a source of strong differential selection for the incipient species to develop specific pollination systems was provided by preexisting and independently established pollination guilds involving long-tongued flies in the families Nemestrinidae and Tabanidae. An increase in tube length would enable a generalist species to enter one of these guilds by excluding insects with shorter tongues from competing for nectar resources. A

decrease in tube length would facilitate the development of a generalist or bee-dominated pollination system. Shifts between the two long-tongued fly pollination systems require only a change in flower color, and plant species can thus shift readily between them. The minor morphological changes required to accomplish a shift between these pollination systems seem to have permitted rapid establishment of reproductive isolation between the diverging populations. Early stages in floral divergence by pollinator-directed disruptive selection are evident in *L. pyramidalis*. The two subspecies are characterized by differences in floral morphology (scent, flower color, tube length), which, although minor, enable them utilize different pollination systems.

Although prepollination isolating mechanisms include seasonal and habitat differences, as well as the use of different pollinators or different body parts of the same pollinator (Levin, 1978), separation in flowering period between related species pairs has not developed in subgenus *Lapeirousia*. This is probably due to the short rainy season and hence short period for biological activity for most organisms in western southern Africa.

Species of subgenus *Lapeirousia* with the same flower type and which belong to the same pollination guild rarely co-occur. In the few instances where two species with flowers of the same general type grow together (e.g., *L. jacquinii* and *L. violacea*; *L. fabricii* and *L. anceps*), the two differ in their chromosome number and no hybrids have been located (Goldblatt et al., 1995). We suggest that one consequence of this genetic isolation was that the genotype of populations colonizing new habitats would not be swamped by neighboring populations with a different chromosome number even in the absence of different pollination systems. A decrease in chromosome number characterizes the clades defined by nodes 2 and 13. These clades may thus represent repeated bursts of parallel radiation from founder species that had become genetically isolated from the ancestral stock.

Despite marked differences in floral morphology between closely related species in subgenus *Lapeirousia*, comparisons of biological differences within species pairs in the subgenus indicate that the diversity of flower types and pollination strategies occurred *after* the differentiation of local populations to new habitats. We hope that the hypotheses about phylogenetic relationships presented here will be compared with phylogenetic reconstructions based on independent molecular methods of DNA sequencing or restriction enzyme analysis.

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- Appendix. Character states and character polarization. The outgroup for character polarization is *Lapeirousia* subg. *Paniculata*. For character 25, used in a secondary analysis (Fig. 3), the outgroup is *Savannosiphon*.
1. On the basis of outgroup comparison the woody corm tunics of subgenus *Lapeirousia* are apomorphic (1). Corm tunics of densely compacted fibers are characteristic of subgenus *Paniculata* (and of the related genera *Thereianthus* and *Micranthus*) (Goldblatt & Manning, 1990).
 2. Entire to lobed corm bases characterize the species of subgenus *Paniculata* and several in subgenus *Lapeirousia*. Minutely serrated (denticulate) tunic bases occur in a number of species (Goldblatt, 1972), and the development of short spines (short-dentate) occurs in *L. divaricata* and its close ally *L. spinosa*, while *L. dolomitica*, *L. violacea*, and *L. tenuis* have long spines extending from the corm bases. The nature of the corm bases is treated as a multistate character with denticulate scored as (1), short-dentate as (2), and long-dentate as (3). The degree of serration, minutely toothed to short- or long-dentate, is regarded as additive and hence ordered.
 3. Campanulate-shaped corms occur in all species of subgenus *Paniculata* and are regarded as plesiomorphic. Apomorphic broadly conic corms are found in three species of subgenus *Lapeirousia*, *L. tenuis*, *L. dolomitica*, and *L. violacea*.
 4. The plesiomorphic condition in subgenus *Paniculata* is probably an actinomorphic flower (Goldblatt & Manning, 1990; Goldblatt & Takei, 1993), but we are sufficiently uncertain about the state in the outgroup that we prefer to score the character as (?). Most species of subgenus *Lapeirousia* have zygomorphic flowers, but four species that also have the aerial stem reduced (thus acaulescent) have actinomorphic flowers. Elsewhere the actinomorphic flower has been interpreted as a reversal from the zygomorphic condition, attendant on the acaulescent habit (Goldblatt, 1972, 1990b).
 5. The acaulescent habit and densely tufted growth habit characterize four species of subgenus *Lapeirousia* (Goldblatt, 1972, 1990b). In these species the habit is constant irrespective of rainfall and other environmental conditions. Species such as *L. silenoides* are acaulescent under adverse conditions, and even *L. exilis*, normally acaulescent, will develop aerial stems under optimal conditions. The acaulescent growth form is unknown in subgenus *Paniculata* or in any other genus of tribe Watsonieae and must be regarded as apomorphic.
 6. The seed surface cells in subgenus *Paniculata* and the closely related genus *Savannosiphon*, possibly the sister genus to *Lapeirousia* (Goldblatt, 1989), are lightly and irregularly colliculate-foveate and the cells are not arranged in regular files (Goldblatt & Manning, 1992). In subgenus *Lapeirousia* most species have seed surface cells in straight files and the epidermal cells are often strongly and regularly colliculate, scored as (1), or tuberculate, scored as (2), both presumably derived states. The patterning is such that species can immediately be placed in groups according to seed surface. A few species of subgenus *Lapeirousia* have the plesiomorphic seed surface type (see data matrix). Both subspecies *pyramidalis* and subspecies *regalis* are scored as having the tuberculate condition. Seed surface cells of *L. fabricii* are also sometimes weakly tuberculate but are more often colliculate, and the species is scored as having the colliculate pattern (alternate scoring produced no change in the topology of the strict consensus tree but it is one step longer).
- It may be argued that the irregular or regular ordering

of cells in files and the surface sculpturing are separate characters, but they are fully correlated, and hence we prefer to treat them as a single one. The extent to which the surface cell wall is raised, either moderately (colluculate), or strongly, especially toward the center (tuberculate), is regarded as additive and hence this multistate character is ordered.

7. Seeds with primary surface sculpturing are rare in *Lapeirousia*, and seeds in subgenus *Paniculata* are globose, the plesiomorphic condition, except in *L. otaviensis* R. Foster and *L. neglecta* Goldblatt & Manning, which have seeds with a ruminant primary sculpturing (unpublished data). In subgenus *Lapeirousia* the seed surface is ridged in a diffuse ruminant pattern in *L. plicata* and *L. odoratissima*, scored as (1), and has a reticulate pattern in *L. oreogena* and *L. montana*, scored as (2). The character states are treated as additive with the diffuse pattern seen as a less specialized type of sculpturing than the very regular reticulate pattern.

8. Strongly developed winglike ridges are present on the locular sutures of the capsules of *Lapeirousia silenoides*, *L. verecunda*, and *L. pyramidalis*. These are regarded as apomorphic, being absent in the outgroup and in other species of subgenus *Lapeirousia*. Likewise, the development of auriculate lobes above the locules on the capsules of *L. arenicola* and *L. macrospatha* must be regarded as derived. Winglike ridges are scored as (1) and auricular lobes as (2), and the character is treated as unordered.

9. Production of branches mostly or entirely near ground level is characteristic of a few species of subgenus *Lapeirousia*, including *L. jacquinii*, *L. pyramidalis*, *L. silenoides*, and *L. verecunda*, and is regarded as derived. The plesiomorphic condition, branching of the flowering stem above ground level, occurs in all species of subgenus *Paniculata* and several of subgenus *Lapeirousia*. The acaulescent species all branch from the base by default because the aboveground internodes are contracted.

10. Genucinate lower tepals (with a sharp bend near the midline) are treated as apomorphic. In *Lapeirousia* the character is restricted to a handful of species of subgenus *Lapeirousia* and is not known at all in subgenus *Paniculata*, in which the lower tepals are straight or cupped.

11. Plicately ribbed leaves are apomorphic for subgenus *Lapeirousia* (Goldblatt & Manning, 1990). The plesiomorphic condition for *Lapeirousia* is a plane leaf. A few species of subgenus *Paniculata* have terete leaves, a secondary condition.

12. Firm-textured floral bracts are characteristic of the species of subgenus *Lapeirousia* and contrast with the soft-textured bracts of section *Paniculata*. Firm-textured bracts also occur in section *Fastigiata* of subgenus *Paniculata*, and appear to be derived here. Based on outgroup comparison, the firm-textured bracts of subgenus *Lapeirousia* are regarded as derived.

13. The perianth tube is shorter to about as long as the tepals in most species of subgenus *Paniculata*, and this is assumed to be the plesiomorphic condition. A tube longer than the tepals is regarded as apomorphic; a tube shorter than the tepals is scored as (1); a tube slightly longer, to 2–3 times as long as the tepals is scored as (2); a tube (3–)4–6 times as long as the tepals is scored as (3).

14. The development of a perianth tube with an abruptly widened throat or gullet is restricted to a few species of subgenus *Lapeirousia* (*L. fabricii*, *L. barklyi*, *L. divaricata*, *L. spinosa*). Species of subgenus *Paniculata* mostly have a uniformly cylindrical tube, sometimes gradually

widened toward the apex, or a widely funnel-shaped tube. Based on outgroup comparison we assume the gullet in subgenus *Lapeirousia* to be derived. A widely funnel-shaped tube (present in the actinomorphic-flowered *L. avasmontana*) may be the plesiomorphic state for *Lapeirousia*, and is scored as (0). The more or less cylindrical tube of the zygomorphic-flowered species of subgenus *Paniculata*, as well as in most species of subgenus *Lapeirousia*, is scored as (1) and the presence of a gullet as (2). The character is treated as ordered as we regard the trend in the elaboration of the tube as additive.

15. The predominant perianth color in the outgroup, subgenus *Paniculata*, is blue with white markings outlined in dark blue to purple and is regarded as the plesiomorphic condition. Other colors are scored as follows: predominantly white, sometimes with blue or mauve markings and/or a lilac flush on the reverse of the tepals (1); white to cream to ivory with red markings on the lower tepals, and on the reverse of the tube and sometimes of the tepals (2); shades of dark red to purple or violet to blue, in either case with contrasting white markings (3). The character states are unordered.

16. Based on outgroup comparison the more or less spatulate tepals of *Lapeirousia silenoides*, *L. verecunda*, and *L. exilis* are apomorphic. The plesiomorphic condition, ovate to lanceolate tepals, characterizes the species of subgenus *Paniculata* and the other species of subgenus *Lapeirousia*.

17. The development of a tooth or ridge of raised tissue at or near the base of each of the lower tepals is an unusual character and, based on outgroup comparison, derived. Filiform teeth occur in *Lapeirousia anceps*, *L. fabricii*, *L. simulans*, *L. macrospatha*, and are weakly developed in *L. jacquinii*. Ridged teeth occur in *L. divaricata*, *L. spinosa*, and *L. barklyi*. We assume these structures are homologous and represent two states of the same character; filiform teeth are scored (1), and ridged teeth as (2).

18. Erect to arched upper tepals, restricted to a few species of subgenus *Lapeirousia*, are regarded as derived. Species of subgenus *Paniculata* and many of subgenus *Lapeirousia* have all the tepals extended and lying in more or less the same plane.

19. Bracts strongly folded in the midline or keeled, present in several species of subgenus *Lapeirousia*, are treated as derived; the bracts of subgenus *Paniculata* are neither folded nor keeled.

20. The inner floral bracts are about as long as to slightly shorter (but narrower) than the outer bracts in all species of the outgroup. Species of subgenus *Lapeirousia* always have the inner bracts about half as long as the outer or less, hence are regarded as apomorphic for the character.

21. Small to moderate sized flowers (excluding the perianth tube) are most likely plesiomorphic for the outgroup (upper tepal less than 18 mm long). A few species of subgenus *Lapeirousia*, notably *L. fabricii* and *L. barklyi*, have notably larger flowers, the upper tepals being 18–27 mm long, a condition regarded as apomorphic.

22. Strongly obtuse to retuse bracts are a feature of two taxa of subgenus *Lapeirousia*, *L. pyramidalis* subsp. *pyramidalis* and *L. pyramidalis* subsp. *regalis*, and the condition is regarded as apomorphic. Bracts are acute in other species of the subgenus and in subgenus *Paniculata*.

23. Scented flowers of, for example, *L. pyramidalis* subsp. *pyramidalis*, *L. divaricata*, and *L. odoratissima* are regarded as derived. Scented flowers are rare in subgenus

Paniculata and are apomorphic within the subgenus. There is no information available about scent chemistry in *Lapeirousia*, and although scents may differ in subgenus *Lapeirousia* we simply score presence or absence of any scent.

24. In subgenus *Paniculata* (and most species of subg. *Lapeirousia*) the lower and upper lateral tepals separate

from the tube at about the same level, the plesiomorphic condition. In *L. divaricata* and *L. spinosa* the lower and upper lateral tepals are united for 3–5 mm, apomorphic for these two species.

25. For the analysis with *Savannosiphon* as outgroup. Corms with flat bases are unique in Iridaceae to *Lapeirousia* and thus scored as apomorphic (1).